New Species of Mammals from Northern South America: Fruit-Eating Bats, Genus *Artibeus* Leach

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ABSTRACTS

The larger species of *Artibeus* of the Amazon Basin are defined, and a new giant species is named and described from Venezuela and Colombia. *Artibeus fallax, A. hercules,* and *A. planirostris* are regarded as subspecies of *Artibeus jamaicensis,* by far the most variable of the larger *Artibeus* of the region.

The smaller *Artibeus* are keyed and arranged in six species groups. A new dwarf species is described from Brazil, Ecuador, Guyana, Peru, and Venezuela. Distribution and diversity of the smaller species are discussed. *Artibeus cinereus,* once thought to range throughout Central America and much of South America and to include all of the smaller taxa except *A. concolor* and *A. hartii,* is restricted to include only the nominate form and *A. quadrivittatus* of the lower Amazon Basin and adjacent coastal areas.

With these additions and changes in status, at least nine species of *Artibeus* now are known to occur in northeastern South America.

Las especies de gran tarnaño de *Artibeus* de la Cuenca del Río Amazonas son definidas y una nueva especie gigante de Venezuela y Colombia es nombrada y descrita. *Artibeus fallax, A. hercules,* y *A. planirostris* son consideradas como subespecies de *Artibeus jamaicensis,* que es el más variable de los grandes *Artibeus* de la región.

Una clave es preparada para las especies de *Artibeus* menores, y las especies son arregladas en seis grupos. Una nueva especie enana de Brasil, Ecuador, Guyana, Perú, y Venezuela es descrita. La distribución y la diversidad de las especies menores son discutidas. *Artibeus cinereus,* que antes se pensó estaba distribuida en Centro América y una gran parte de Sudamérica, y que incluyera todas las taxa más pequeñas (a excepción de *A. concolor* y *A. hartii*), es ahora restringuida para incluir solamente la especie nominal y *A. quadrivittatus* a la Cuenca baja del Río Amazonas y a las areas costeras adyacentes.

Con estas adiciones y cambios de "status," por lo menos nueve especies de *Artibeus* ya son conocidas y se encuentran en el nordeste de Sudamérica.

São definidas as espécies maiores de *Artibeus* que ocorrem na Bacia Amazônica, e uma espécie nova, gigante, é descrita. *Artibeus fallax, A. hercules,* e *A. planirostris* são consideradas subespécies de *Artibeus jamaicensis,* certamente a espécie mais variável dos *Artibeus* maiores da região.

Uma chave para os *Artibeus* menores, os quais foram designados a seis grupos de espécies, é fornecida. Uma espécie nova aña é descrita do Brasil, Equador, Guiana, Peru, e Venezuela. A diversidade, e as distribuições geográficas destas espécies, são discutidas. *Artibeus cinereus,* o qual acreditava-se abranger toda América Central e grande parte da América do Sul, além de incluir todos taxa menores com excessão de *A. concolor* e *A. hartii,* é reduzido a um único taxon, restrito ao sul da Bacia Amazônica e às suas áreas adjacentes.

Incluindo as adições e mudanças de status propostas neste trabalho, são reconhecidas, atualmente, ao menos nove espécies de *Artibeus* na região nordeste da América do Sul.

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Introduction

Mammals and their ectoparasites were collected in Venezuela between 1965 and 1968 by the Smithsonian Venezuelan Project (SVP), supported in part by a contract (DA-49-MD-2788) of the Medical Research and Development Command, Office of the Surgeon General, U.S. Army. Numerous papers have described the ectoparasites and mammals of the Project. Throughout these papers undescribed species of mammals have been referred to by alphabetical designations. Some of these have been named subsequently by Handley and Ferris (1972), Handley and Gordon (1980), and Handley (1984). This paper deals with fruit-eating bats of the genus *Artibeus* Leach.

The cranial measurements reported here were taken as outlined by Handley (1959, p. 98). Hind foot, tibia, calcar, and forearm were measured on dry museum specimens or on specimens preserved in alcohol; all other external dimensions were measured on fresh specimens in the field. All measurements are in millimeters. Coloration was determined under Examolites (Macbeth Corp., Newburg, NY 12533) with natural light excluded.

A New Giant *Artibeus*

It is now generally agreed that in and around the Amazon Basin there are three large species of *Artibeus*. Handley (1976) recognized them as: (1) *A. fuliginosus* Gray—smaller, molars 3/3, rostrum arched, postorbital process poorly developed, fur long, coloration blackish, facial stripes faint or absent, interfemoral membrane (IM) naked; (2) *A. jamaicensis* Leach—larger, molars 3/3, rostrum arched, postorbital process poorly developed, fur short, coloration gray-brown, facial stripes present but not sharply defined, IM naked; and (3) *A. lituratus* Olfers—larger, molars 2/3, rostrum flattish, postorbital process well developed, fur short, coloration chocolate brown, facial stripes prominent and well defined, IM hairy. However, as shown by Koopman (1978) and Honacki et al. (1982), there is no consensus on the delimitation of these species.

The difficulty in defining the species arises primarily from the fact that *Artibeus jamaicensis* is unusually variable geographically in morphology. The other species show very little variation in this region. *Artibeus jamaicensis* is large in the Amazon Basin, so large in fact that the subspecies there, *A. j. fallax* Peters and *A. j. hercules* Rehn, until recently have been aligned by most authors with the universally large *A. lituratus*, although they differ from it in many characteristics other than size. To the southeast of the Amazon Basin (*A. j. planirostris* Spix) and to the north of it (*A. j. trinitatis* Andersen), *A. jamaicensis* is dramatically smaller, in fact similar in size to *A. fuliginosus*. Everywhere east of the Andes *A. jamaicensis* has 3/3 molars; west of the Andes and in Central America it has 2/3 molars.

Specimens in the SVP collection show that the large *Artibeus jamaicensis fallax* and small *A. j. trinitatis* apparently intergrade in the Llanos of Venezuela where the habitat is marginal for *A. jamaicensis* and where it is an uncommon bat. Furthermore, intergradation between the small, 12-molar *A. j. trinitatis* and the slightly larger, 10-molar *A. j. aequatorialis* Andersen of the northwest coast of South America can be seen in specimens from northern Colombia.

These two zones of intergradation are of crucial importance in the nomenclature of *Artibeus*, for they serve to link "*A. jamaicensis*" of the West Indies and Central America and "*A. planirostris*" of eastern South America. They are especially important in the present context because of the discovery of a fourth large *Artibeus*, superficially similar to but larger than *A. j. fallax*, occurring together with it in southern Venezuela and with the small *A. j. trinitatis* in western Venezuela and northern Colombia. It can be recognized as follows:

Artibeus amplus new species

HOLOTYPE—USNM 440932, adult female with suckling young, skin and skull, collected 15 April 1968 by Norman E. Peterson, F. P. Brown, Jr., and J. O. Matson at Kasmera, 21 km SW Machiques, Estado Zulia, Venezuela, 270 m, in a damp cave in a cliff across the Río Yasa from the Kasmera Biological Station, eastern foothills of the Sierra de Perijá. Original number, SVP 22086.

ETYMOLOGY—Latin *amplus*, large, referring to the large size of this bat, one of the largest *Artibeus*.

DISTRIBUTION—Northern foothills of the Central Andes in Colombia; lower eastern slopes of the Sierra de Perijá and the Venezuelan Andes in western Venezuela; and the vicinity of Cerro Duida and the low mountains of southeastern Bolívar in southern Venezuela. It probably occurs in ad-

jacent parts of Guyana and Brazil as well. The SVP collectors found *A. amplus* near streams and in other moist areas (98%); in evergreen forest (90%) and in forest openings such as yards and orchards (10%). Most specimens were mist netted (86%), but some (14%) were found roosting in the twilight zone of caves. Elevational range, 24–1200 m. Holdridge life zones (Ewel & Madriz, 1968): Tropical humid forest (10%), Tropical very humid forest (22%), Premontane humid forest (12%), Premontane very humid forest (2%), Premontane rain forest (4%), Lower montane very humid forest (10%), and Lower montane rain forest (40%). Ridge slopes and valley floor in the area where the holotype was collected were clothed with second growth evergreen forest, while lawns, shrubbery, banana and papaya plants, and scattered grapefruit trees characterized the grounds of the biological station.

DESCRIPTION—Size large (forearm 70.0, greatest length of skull 31.3, maxillary toothrow 11.2—averages of Venezuelan specimens). Coloration of fur as in sympatric *Artibeus jamaicensis* (dorsum blackish brown to brown; facial stripes present but obscure; underparts blackish brown, usually frosted with white; underarms with abundant long, usually whitish hairs); ears dark fuscous to black, paler basally; lips and noseleaf blackish; membranes blackish; wing tips undifferentiated or grayish, never white. Horseshoe of noseleaf bound down mediobasally; legs and interfemoral membrane slightly hairy, the latter particularly medioventrally, where hairs extend as a short fringe beyond edge of membrane; forearm long.

Skull superficially like that of *Artibeus jamaicensis,* but relatively longer and narrower; rostrum long and flattish; supraorbital ledges subparallel and together with postorbital processes often poorly developed or even ill-defined; zygomata not very flared from skull, usually subparallel to one another, and in side view, thin and fragile; posterolateral angle of skull not particularly flared; palate relatively narrow and toothrows ovoid in outline; postpalatal extension usually long, narrow, and parallel sided; dentition as in *A. jamaicensis,* except I^1 only weakly bilobed; dental formula 2/2–1/1–2/2–3/3 × 2 = 32. This bat is the only known host of *Strebla paramirabilis* Wenzel and *Trichobius assimilis* Wenzel (Diptera: Streblidae), so it can be distinguished from other *Artibeus* by its parasites as well as its morphology.

Measurements of the holotype, an adult female: total length 101, tail vertebrae 0, hind foot (dry) 17, ear from notch 25, forearm 69.2, tibia 24.1, calcar 6.2, weight 70.4 g. Greatest length of skull 31.9, zygomatic breadth 18.3, postorbital breadth 7.7, breadth of braincase 13.3, depth of braincase 11.6, length of maxillary toothrow 11.2, postpalatal length 9.8, palatal breadth outside of M^3 12.9, rostral breadth at base of canines 8.3. See Table 1 for additional measurements.

COMPARISONS—Four large species of *Artibeus* occur in Venezuela, all of them together in the southern part of the country. Among these, *Artibeus amplus* and *A. jamaicensis* are most alike; but despite the superficial resemblance, the two can be distinguished by many characters, both external and cranial. All *A. amplus* examined have the lower edge of the noseleaf horseshoe bound down, while about 95% of *A. jamaicensis* from the same localities have it free; all *A. amplus* have the interfemoral membrane slightly hairy and fringed medially, but *A. jamaicensis* never does; and while *A. jamaicensis* often has the wings white-tipped, *A. amplus* never does. Cranially, *A. amplus* differs from *A. jamaicensis* in having a longer, narrower skull; longer, somewhat more flattened rostrum (most easily seen in dimensions of rostral shield); less arched nasals; margins of supraorbital nearly parallel, rather than converging posteriorly, and usually not as well developed; zygomata thinner and more fragile and usually subparallel rather than diverging markedly posteriorly; posterolateral angle of skull not so flaring; palate narrower and toothrows usually less nearly circular in outline; and postpalatal extension usually longer and narrower, parallel sided (not flaring posteriorward). The two species are hosts of different species of parasitic streblid flies.

SPECIMENS EXAMINED—Total 55. **COLOMBIA. Antioquia:** La Tirana, 33 km SW Zaragoza, 520 m (2 USNM). **VENEZUELA. Apure:** Nulita, Selvas de San Camilo, 29 km SSW Santo Domingo, 24 m (2 USNM). **Bolívar:** 21 to 33 km NE Icabarú, 775–851 m (6 USNM); Km 125, 85 km SSE El Dorado, 826–1165 m (5 USNM). **T.F. Amazonas:** Belén, Río Cunucunuma, 56 km NNW Esmeralda, 150 m (9 USNM); Cabecera del Caño Culebra, Cerro Duida, 40 km NNW Esmeralda, 1140–1200 m (21 USNM); Caño Culebra, Cerro Duida, 50 km NNW Esmeralda, 800 m (2 USNM); Tamatama, Río Orinoco, 2 km above Boca del Casiquiare, 135 m (2 USNM). **Zulia:** Kasmera, 21 km SW Machiques, 270 m (3 USNM, 1 UCV); 15 km W Machiques (1 AMNH); Novito, 19 km WSW Machiques, 1135 m (1 USNM).

REMARKS—In previous publications of SVP, *Artibeus amplus* has been known as "*Artibeus* sp. D".

TABLE 1. Measurements of adult *Artibeus amplus* and *A. jamaicensis*. For each measurement, line 1 includes the mean plus or minus two standard errors, line 2 the extremes, and line 3, in parentheses, the number of specimens measured. All specimens are from Venezuela unless otherwise stated.

Total length	Hind foot (dry)	Ear	Forearm	Greatest length	Zygomatic breadth	Postorbital breadth
			Artibeus amplus, males and females, Zulia and Colombia			
100.4 ± 3.88	18.4 ± 0.60	23.7 ± 1.28	70.8 ± 1.78	31.4 ± 0.26	18.6 ± 0.20	7.9 ± 0.20
93–104	17–19	22–26	68.6–75.3	31.0–31.9	18.1–18.8	7.6–8.3
(5)	(7)	(7)	(7)	(7)	(7)	(7)
			A. amplus, males and females, T.F. Amazonas and Bolívar			
89.9 ± 2.22	18.3 ± 0.30	23.0 ± 0.98	69.1 ± 0.90	31.2 ± 0.24	18.4 ± 0.14	7.8 ± 0.10
80–100	17–20	18–26	65.0–73.2	30.3–32.8	17.4–19.1	7.3–8.4
(21)	(22)	(21)	(22)	(29)	(30)	(31)
			A. jamaicensis, females, Zulia			
86.4 ± 2.90	15.9 ± 0.40	22.6 ± 0.96	61.1 ± 0.64	27.7 ± 0.24	16.9 ± 0.30	6.8 ± 0.08
77–95	14–18	17–25	58.9–64.2	26.7–28.5	16.0–17.7	6.5–7.1
(19)	(19)	(19)	(19)	(19)	(12)	(19)
			A. jamaicensis, males, Zulia			
83.8 ± 4.14	15.4 ± 0.32	22.2 ± 0.98	59.3 ± 0.92	27.4 ± 0.14	17.0 ± 0.28	6.8 ± 0.14
73–91	15–16	20–25	56.2–61.4	27.1–27.7	16.6–17.6	6.3–7.0
(10)	(10)	(10)	(10)	(10)	(6)	(10)
			A. jamaicensis, females, T.F. Amazonas			
88.1 ± 1.62	17.8 ± 0.32	24.6 ± 0.46	66.8 ± 1.12	30.7 ± 0.28	19.1 ± 0.14	7.5 ± 0.10
80–93	16–19	23–26	62.1–70.1	29.4–31.3	18.7–19.6	7.1–7.7
(17)	(17)	(17)	(17)	(14)	(13)	(14)
			A. jamaicensis, males, T.F. Amazonas			
86.3 ± 1.60	18.3 ± 0.32	24.6 ± 0.52	65.4 ± 1.42	30.7 ± 0.26	19.3 ± 0.32	7.6 ± 0.16
82–90	18–19	24–26	62.4–68.6	30.2–31.4	18.6–20.2	7.2–7.9
(8)	(8)	(8)	(8)	(8)	(8)	(8)

A New Dwarf *Artibeus*

The taxonomy of the smaller *Artibeus* is in a state of flux. As recently as 35 years ago all of the smaller species except *A. concolor* Peters and *A. hartii* Thomas were believed to be variants of *A. cinereus* Gervais. Since then, first one and then another of the supposed subspecies of *A. cinereus* has been shown to be independent species. Today only *A. bogotensis* Andersen, *A. glaucus* Thomas, *A. pumilio* Thomas, *A. quadrivittatus* Peters, *A. rosenbergi* Thomas, and *A. watsoni* Thomas remain associated with *A. cinereus* (Honacki et al., 1982). However, except for *A. quadrivittatus*, these do not properly belong with *A. cinereus* either.

Artibeus glaucus and *A. bogotensis* intergrade in Ecuador and form an Andean-northern South American species sympatric with *A. cinereus* in southern Venezuela. *Artibeus glaucus* thus has two subspecies, the nominate form and *A. g. bogotensis*. *Artibeus watsoni* Thomas of northwestern South America and Central America is closely related, but intergradation with *A. g. glaucus* or *A. g. bogotensis* has not been observed.

Artibeus pumilio is an enigmatic taxon. Many museum specimens bear the name *A. pumilio*, but perhaps the only specimen properly associated with the name is the holotype. This specimen may be only an odd variant of one of the other species, but not of the species described here. For the present, *A. pumilio* must be regarded as unplaceable. The same can be said for *A. rosenbergi*, characterized by a curiously long, narrow skull such as can be found occasionally in large samples of most species of *Artibeus*. Because of their equivocal status, neither *A. pumilio* nor *A. rosenbergi* is included in the appended list of species and key. The characteristics and status of these taxa will be the subject of another paper.

Thus, *A. cinereus* now has been shorn of all of its supposed subspecies except *A. c. quadrivittatus*. Its supposed range has been reduced from encompassing most of Central America and tropical South America to occupying only the Amazon Basin (possibly only the lower basin) and adjacent coastal areas. Sympatric with *A. cinereus* in much of its range is a distinctive dwarf species which can be known as:

TABLE 1. *Continued.*

Braincase breadth	Braincase depth	Maxillary toothrow	Postpalatal length	Width at molars	Width at canines	Tibia
			Artibeus amplus, males and females, Zulia and Colombia			
13.5 ± 0.20 13.2–14.0 (7)	11.0 ± 0.26 10.6–11.6 (7)	11.2 ± 0.16 11.1–11.5 (7)	9.7 ± 0.20 9.3–10.0 (7)	13.2 ± 0.26 12.7–13.5 (7)	8.4 ± 0.16 8.2–8.8 (7)	25.9 ± 1.28 24.1–28.2 (6)
			A. amplus, males and females, T.F. Amazonas and Bolívar			
13.3 ± 0.12 12.9–14.0 (30)	11.2 ± 0.06 10.7–11.5 (30)	11.2 ± 0.10 10.7–11.8 (31)	9.8 ± 0.14 9.1–10.6 (28)	13.3 ± 0.10 12.8–13.9 (30)	8.6 ± 0.08 8.3–8.9 (30)	24.8 ± 0.38 23.1–26.2 (22)
			A. jamaicensis, females, Zulia			
12.3 ± 0.10 12.0–12.8 (19)	10.2 ± 0.16 9.5–10.9 (19)	10.0 ± 0.12 9.4–10.5 (17)	8.6 ± 0.14 8.2–9.3 (18)	12.1 ± 0.16 11.2–12.7 (19)	7.6 ± 0.10 7.2–8.0 (19)	22.4 ± 0.50 20.1–23.8 (19)
			A. jamaicensis, males, Zulia			
12.1 ± 0.14 11.8–12.4 (10)	10.3 ± 0.18 10.0–10.9 (10)	10.1 ± 0.16 9.7–10.4 (8)	8.4 ± 0.12 8.2–8.8 (10)	12.2 ± 0.18 11.8–12.6 (10)	7.7 ± 0.12 7.4–7.9 (9)	21.7 ± 0.52 20.1–23.0 (10)
			A. jamaicensis, females, T.F. Amazonas			
13.2 ± 0.12 12.9–13.5 (14)	10.8 ± 0.18 10.2–11.5 (14)	11.4 ± 0.20 11.0–12.0 (13)	9.4 ± 0.18 8.9–10.0 (14)	13.7 ± 0.22 13.2–14.4 (13)	8.6 ± 0.12 8.3–8.9 (13)	24.1 ± 0.46 22.3–25.4 (17)
			A. jamaicensis, males, T.F. Amazonas			
13.4 ± 0.22 12.8–13.7 (8)	11.0 ± 0.18 10.7–11.4 (8)	11.4 ± 0.18 11.1–11.8 (8)	9.3 ± 0.24 8.7–9.8 (8)	13.8 ± 0.30 13.0–14.3 (8)	8.8 ± 0.12 8.6–9.1 (8)	23.3 ± 0.52 22.0–24.4 (8)

Artibeus gnomus new species

HOLOTYPE—USNM 387534, adult female, skin and skull, collected 14 June 1966 by A. L. and M. D. Tuttle at El Manaco (= Km 74), 59 km SE El Dorado, Bolívar, Venezuela, 150 m, in a mist net in an orchard. Original number, SVP 9298.

ETYMOLOGY—Latin *gnomus*, diminutive fabled being, dwarf, alluding to the small size of this species, one of the smallest *Artibeus*.

DISTRIBUTION—The Amazon Basin and bordering regions; from northern Amazonas Territory (14 km SSE Pto. Ayacucho) and northern Bolívar State (28 km SE El Manteco) in Venezuela and northern Guyana, to Pará (Belém) and Mato Grosso (Serra do Roncador), Brazil, and Loreto (Santa Rosa), Peru. SVP collectors netted *A. gnomus* mostly in moist sites (92%) in evergreen forest (52%) or openings such as savannas (25%) and yards and orchards (23%). Elevations range 119–161 m in Venezuela, sea level to 530 m in Brazil. Holdridge life zones: Tropical dry forest (22%), Tropical humid forest (67%), Tropical very humid forest (2%), and Premontane humid forest (9%).

DESCRIPTION—Body size small (forearm averages 36–38, greatest length of skull 18.5–18.7, and maxillary toothrow 5.7–6.0). Dorsal coloration gray-brown to brown; underparts paler; facial stripes very white and sharply defined. Soft parts coloration in life (USNM 361742, male, Belém, Brazil): ear narrowly edged with yellow, brightest toward base; antitragus entirely yellow; tragus yellow, brightest distally and on posterior basal lobe; noseleaf and horseshoe gray-brown medially, cream color laterally; lips and chin gray-brown; iris brown; forearm and fingers brownish flesh color; wings blackish, except membrane between fingers II and III transparent, grayish; interfemoral membrane sooty brown; legs and feet dark brown; claws horn color. Face short; shape and proportions of ears, noseleaf, horseshoe, lips, chin, and interfemoral membrane as in *Artibeus cinereus*; noseleaf minutely hirsute; lower edge of horseshoe free; basal part of forearm hairy; hind extremities (except for short hairs on feet) appear naked.

Skull small, short, and broad; zygomata subparallel; rostrum narrow, very short, moderately

TABLE 2. Measurements of adult male and female (combined) *Artibeus gnomus* and *A. glaucus bogotensis*. For each measurement, line 1 includes the mean plus or minus two standard errors, line 2 the extremes, and line 3, in parentheses, the number of specimens measured. All specimens are from Venezuela.

Total length	Hind foot (dry)	Ear	Forearm	Greatest length	Zygomatic breadth	Postorbital breadth
Artibeus gnomus, Río Supamo, Los Patos, and El Manaco						
47.5 ± 1.40	9.5 ± 0.28	16.9 ± 0.62	36.7 ± 0.54	18.5 ± 0.18	11.0 ± 0.18	4.9 ± 0.10
44–54	9–10	14–19	34.0–38.3	17.9–19.1	10.4–11.2	4.5–5.2
(13)	(13)	(13)	(13)	(14)	(8)	(14)
A. glaucus bogotensis, Km 125, 85 km SSE El Dorado						
52.2 ± 0.86	10.6 ± 0.22	17.4 ± 0.38	39.6 ± 0.60	20.3 ± 0.10	11.6 ± 0.10	5.0 ± 0.04
49–56	10–11	16–19	36.8–41.9	19.4–21.2	10.8–12.1	4.6–5.3
(19)	(19)	(19)	(19)	(50)	(44)	(51)

deep and arched, and much swollen posterolaterally (part on rostral shield, part within orbit, above eye); excavation for orbital nerve large and deep; braincase short and deep, with swelling at posterodorsal apex interrupting junction of sagittal and lambdoidal crests; postpalatal extension relatively short; internal edge of pterygoid fossa strongly ridged, narrowing mesopterygoid fossa and cupping pterygoid fossa which opens straight back; vomerine ridge visible in mesopterygoid fossa; vacuities in roof of posterior nares much anterior to mesopterygoid fossa and not easily seen; outline of maxillary toothrows nearly circular; upper canine small (especially in basal diameter); M^1 with accessory internal ridge on lateral cusps, and with relatively wide talon; m_3 present (75 of 79 specimens examined).

Measurements of the holotype, an adult female: total length 47, tail vertebrae 0, hind foot (dry) 9, ear from notch 18, forearm 36.5, tibia 12.6, calcar 4.9, weight 10.5 g. Greatest length of skull 18.2, zygomatic breadth 10.8, postorbital breadth 4.8, breadth of braincase 8.5, depth of braincase 7.2, length of maxillary toothrow 5.5, postpalatal length 6.5, palatal breadth outside of M^3 7.1, rostral breadth at base of canines 4.6. See Table 2 for additional measurements.

COMPARISONS—*Artibeus gnomus* differs from *A. concolor* and *A. hartii* in many ways, but most significantly in lack of M^3. From all other small *Artibeus* (*A. anderseni, A. cinereus,* and *A. glaucus bogotensis*) that occur within its range, *A. gnomus* can be distinguished by its possession of m_3. Among the specimens examined, m_3 is consistently absent in these other taxa while it is consistently present in *A. gnomus* (except in southern Venezuela, where it is absent from both mandibles in four of 53 specimens and from one mandible only in two others). In addition, *A. gnomus* differs from all of the sympatric taxa in its more prominent white facial stripes; more colorful ears, noseleaf, and lips; average browner, less grayish coloration of pelage; shorter face and rostrum (except when compared with *A. concolor*); more swollen supraorbital region; average larger and deeper orbital nerve excavation (sometimes equally large and deep in *A. g. bogotensis*); and more cupped pterygoid fossa, with internal ridge so enlarged as to significantly narrow the mesopterygoid fossa.

Artibeus gnomus differs from the sympatric taxa individually in several other ways. It is much smaller than *A. concolor* (forearm averages 36–38 vs. 46–48). In contrast to *A. hartii* it has notched inner upper incisors, brownish rather than dark chocolate coloration, and a wide, unfringed interfemoral membrane. Compared with *A. anderseni* (including the holotype, FMNH 21331), *A. gnomus* is similar in size (slightly larger than Rio Madeira *A. anderseni*); has rostrum much deeper, more arched, narrower, and shorter; face not dished; orbit larger; zygomata more nearly parallel; and vacuities in roof of posterior nares far forward of mesopterygoid fossa, rather than opening in it or close to it.

At Belém, Brazil, both *Artibeus gnomus* and *A. cinereus* were numerous and were often taken in the same nets. There, fresh specimens of the two species were compared. *Artibeus gnomus* is smaller in size, and has a smaller head and shorter face; facial stripes much brighter, more sharply defined, and more prominent; ears, noseleaf, and lips more brownish, less grayish; ear edgings, antitragus, and tragus bright yellow, rather than cream; and noseleaf edged with cream, rather than plain gray-brown. Furthermore, it has zygomata more nearly parallel; rostrum deeper and shorter; supraorbital area much swollen and its edges nearly parallel; and smaller teeth.

TABLE 2. *Continued.*

Braincase breadth	Braincase depth	Maxillary toothrow	Postpalatal length	Width at molars	Width at canines	Tibia
			Artibeus gnomus, Río Supamo, Los Patos, and El Manaco			
8.5 ± 0.14	7.4 ± 0.14	5.7 ± 0.06	6.3 ± 0.10	7.5 ± 0.12	4.9 ± 0.08	13.2 ± 0.46
8.1–9.0	7.1–8.0	5.5–5.9	6.0–6.7	7.1–7.9	4.6–5.1	11.2–14.4
(14)	(14)	(14)	(14)	(14)	(14)	(13)
			A. glaucus bogotensis, Km 125, 85 km SSE El Dorado			
9.0 ± 0.06	7.9 ± 0.06	6.5 ± 0.04	7.0 ± 0.08	8.0 ± 0.06	5.1 ± 0.06	13.6 ± 0.36
8.5–9.5	7.2–8.3	6.0–6.8	6.5–7.5	7.5–8.7	4.9–5.6	12.3–15.8
(48)	(48)	(51)	(47)	(50)	(50)	(19)

In southern Venezuela *Artibeus gnomus* is sympatric with *A. glaucus bogotensis.* Compared with Venezuelan specimens and with the holotype (BM 99.11.4.35) of this taxon, *A. gnomus* is much smaller and shorter faced; has a deeper, shorter rostrum; disproportionately wider zygomatic spread; and smaller teeth.

In addition to comparisons of *A. gnomus* with sympatric species, two other small *Artibeus* need to be considered:

1. ***Artibeus g. glaucus***—This species occurs nearby in the Andes. It (including the holotype, BM 94.8.6.13) possesses m_3, and its skull has the basic shape of *A. gnomus.* However, it is much larger and darker in color, has the hind extremities much hairier, the supraorbital region usually less swollen, and the pterygoid fossa much less cupped and opening to the mesopterygoid fossa.

2. ***Artibeus watsoni***—West of the Andes and extending into Central America is another small species, *A. watsoni* Thomas, which like *A. gnomus* possesses m_3. It (including its holotype, BM 0.7.11.19) is larger than *A. gnomus*; has larger teeth; longer rostrum, with reduced supraorbital swelling; shallower and less well-defined orbital nerve excavation; and like *A. glaucus* has the pterygoid fossa not cupped and opening into the mesopterygoid fossa (which consequently is not narrowed by the inner pterygoid ridge).

DISCUSSION—The ten small species of *Artibeus* recognized here can be associated in six species groups:

1. ***Artibeus concolor* Group**—Amazon and upper Orinoco basins and Guianas. Includes only *Artibeus concolor.*

2. ***Artibeus hartii* Group**—Mexico and Central America, across northern South America to Trinidad, and south to Peru east of the Andes and to Ecuador west of the Andes. Includes only *Artibeus hartii.*

3. ***Artibeus glaucus* Group**—Mexico, Central America, and South America to Mato Grosso and Peru. Includes *Artibeus glaucus* (with two subspecies, *A. g. bogotensis* and *A. g. glaucus*), *A. gnomus,* and *A. watsoni.*

4. ***Artibeus toltecus* Group**—Mexico and Central America. Includes *Artibeus aztecus* Andersen and *Artibeus toltecus* Saussure, each with several subspecies.

5. ***Artibeus cinereus* Group**—Guiana region, coastal Brazil, and lower Amazon Basin (dubiously also upper Amazon Basin). Includes only *Artibeus cinereus,* with *A. c. quadrivittatus* as a subspecies.

6. ***Artibeus phaeotis* Group**—Mexico, Central America, and South America to upper Amazon Basin and western Ecuador. Includes *Artibeus anderseni* Osgood and *Artibeus phaeotis* Miller,[1] with several subspecies.

Diversity in the small *Artibeus* is greatest in eastern South America, where representatives of five of the six groups occur and where three of the groups are endemic. Altogether six species occur in and around the Amazon Basin, while only one is known with certainty in the central portion of the Basin; there are three in the lower Amazon

[1] Until recently (Koopman, p. 152, in Honacki et al., 1982) it has not been generally recognized that *Artibeus phaeotis* and *A. ravus* are conspecific. They intergrade in eastern Panama and western Colombia. Both names date from Miller (1902). Although *A. ravus* was named first, on an earlier page, *A. phaeotis* became embedded in the literature as the name of this species.

and on the southern fringes in Brazil and Bolivia, four or five in southern Venezuela, and five in eastern Peru, Ecuador, and Colombia. In contrast, only three of the species groups occur in Central America, and only one of them is endemic there.

Several distributional patterns are represented in the complex of Amazonian species. *Artibeus concolor* is found throughout the Basin but scarcely beyond it; *A. cinereus* occurs in the lower Amazon and along the coast for some distance north and south of the river; *A. anderseni* is known from the upper Amazon and an isolated area in northern Colombia; *A. glaucus* is higher up, in the Andes, and eastward around the northern edge of the Basin in Venezuela; the range of *A. hartii* resembles that of *A. glaucus,* but extends on into Central America; and the dwarf *A. gnomus* has a peculiar circular range, completely ringing the Amazon Basin but apparently not extending into its interior.

Key to the Smaller Species of *Artibeus*

1. Molars 3/3 (m_3 large) 2
1′. Molars 2/3 (m_3 minute) or 2/2 3
2. I^1 notched; facial stripes absent; coloration pale brown; interfemoral membrane broad and naked; forearm 43–52 mm ..... *Artibeus concolor*
2′. I^1 not notched; facial stripes present; coloration dark chocolate brown; interfemoral membrane narrow and fringed; forearm 36–42 mm ..... *Artibeus hartii*
3. Supraorbital region much swollen; molars 2/3 (2/2 in *A. g. bogotensis* and occasionally in the others) ... *Artibeus glaucus* Group, 4
3′. Supraorbital region little, or not at all, swollen; molars 2/2 7
4. Rostrum short and moderately arched; pterygoid fossa cupped and opening back, causing mesopterygoid fossa to be narrowed; forearm 34–38 mm ..... *Artibeus gnomus*
4′. Rostrum long and much or only moderately arched; pterygoid fossa not cupped, opening into and not narrowing mesopterygoid fossa 5
5. Rostrum much arched; orbital nerve excavation shallow and often ill-defined; dorsum pale brownish; ears pale; forearm 35–41 mm ..... *Artibeus watsoni*
5′. Rostrum moderately arched; orbital nerve excavation deep and well defined 6
6. Molars usually 2/3; dorsum dark grayish or blackish; ears dark; forearm 38–42 mm ... . *Artibeus glaucus glaucus*
6′. Molars 2/2; dorsum pale brownish or grayish; ears pale; forearm 37–41 mm .... *Artibeus glaucus bogotensis*
7. Interfemoral membrane narrow and fringed; coloration blackish .... *Artibeus toltecus* Group, 8
7′. Interfemoral membrane broad, naked; coloration brownish 9
8. Larger, forearm 42–48 mm .... *Artibeus aztecus*
8′. Smaller, forearm 37–41 mm .... *Artibeus toltecus*
9. Rostrum deep and arched; palate long and moderately wide ..... *Artibeus cinereus*
9′. Rostrum shallow and flattened; palate short and very wide .... *Artibeus phaeotis* Group, 10
10. Maxillary toothrow 5.2–6.2 mm; rostrum often tilted up anteriorly .... *Artibeus anderseni*
10′. Maxillary toothrow 6.7–7.1 mm; rostrum usually not tilted up anteriorly[2] .... *Artibeus phaeotis*

SPECIMENS EXAMINED—***Artibeus anderseni***—**BRAZIL. Amazonas:** Borba, Rio Madeira (1 AMNH). **Rondônia:** Pôrto Velho (2 AMNH, 2 FMNH, including holotype of *A. anderseni*); Sto. Antonio do Hauayara (4 AMNH). **COLOMBIA. Bolívar:** Catival, Upper Río San Jorge, 120 m (16 FMNH). **Antióquia:** Aljibos, 26 km S and 22 km W Zaragoza, 630 m (2 USNM); nr. La Tirana, 24 km S and 22 km W Zaragoza, 520 m (2 USNM). **ECUADOR. Napo:** Río Suno (Abajo) (4 AMNH). **Pastaza:** Montalvo, Río Bobonaza (1 FMNH); Río Pindo Yacu (1 FMNH); Río Yana Rumi (1 FMNH). **PERU. Huánuco:** Monte Alegre (1 AMNH). **Loreto:** Boca Río Curaray (1 AMNH); Boca Río Peruate, Río Amazonas, 90 m (1 FMNH); Lagarto, Alto Ucayali (1 AMNH); Mazán (1 AMNH); 59 km W Pucallpa (1 USNM); Puerto Indiana, Río Amazonas (2 AMNH); Río Morona (Quebr. Pushaga), Alto Amazonas, 220 m (2 FMNH); Río Yavari Mirim (Quebr. Esperanza), 200 m (2 FMNH); Santa Cecilia, Río Maniti, Iquitos, 110 m (3 FMNH); Santa Luisa, Río Nanay, Iquitos, 160 m (1 FMNH); Sarayacu, Río Ucayali (1 AMNH). **Pasco:** San Juan, Oxapampa,

[2] Couplet 10 will separate *Artibeus anderseni* and *A. phaeotis* in South America and in southern Central America, but it will not distinguish *A. anderseni* from Mexican *A. phaeotis nanus.* In such a comparison, *A. anderseni* can be recognized by its relatively broader skull.

274 m (3 USNM). **Departamento (?):** Yuhucumayo, 1200 ft [= Puno: Yahuaramayo, 366 m?] (1 MCZ).

***Artibeus cinereus cinereus*—BRAZIL. Amazonas:** Sta. Clara, Vila Bela Imperatriz [nr. Parintins] (1 AMNH). **Pará:** Fordlândia, Rio Tapajós (2 AMNH); Maracano, Rio Jamundá [= Nhamundá?], Faro (5 AMNH); Rio Yumundá, Faro (1 BM).

***Artibeus cinereus quadrivittatus*—BRAZIL. Maranhão:** Juryassú [= Turiaçu?] (1 BM). **Pará:** Belém (10 USNM); Benevides (1 BM); Pará [= Belém] (1 BM); Ilha do Taiuna, Rio Tocantins (3 AMNH). Pernambuco: Pernambuco [= Recife] (2 BM). Rio Grande do Norte: Natal (1 USNM). **SURINAME. Surinam** (1 BM). **VENEZUELA. Bolívar:** Hato San Felipe, Serranía de Nuria (1 UCV); Hato San José, 20 km W La Paragua, 300–324 m (2 USNM).

***Artibeus glaucus bogotensis*—COLOMBIA. Cundinamarca:** Bogotá (2 BM); nr. Bogotá (1 BM); Curiche, nr. Bogotá (2 BM, including holotype of *A. bogotensis*); Fómeque (1 AMNH); Fusagasuga (2 MCZ); Río Negro, nr. Bogotá (2 BM). **GUYANA.** Kanuku Mts. (3 BM). **VENEZUELA. Bolívar:** El Manaco, 59 km SE El Dorado, 150 m (3 USNM); Hato San José, 20 km W La Paragua, 300–324 m (3 USNM); 23 to 45 km NE Icabarú, 824–851 m (3 USNM); Km 125, 85 km SSE El Dorado, 826–1165 m (120 USNM); Río Supamo, 50 km SE El Manteco, 150 m (2 USNM). **T.F. Amazonas:** Belén, Río Cunucunuma, 56 km NNW Esmeralda, 150 m (1 USNM); Caño Culebra, Cerro Duida, 50 km NNW Esmeralda, 800 m (3 USNM).

***Artibeus glaucus glaucus*—BOLIVIA. Santa Cruz:** Buenavista, 400 m (1 FMNH). **ECUADOR. Napo:** Baeza (1 BM). **PERU. Cuzco:** Collpa de San Lorenzo, Quincemil, 700 m (11 FMNH); Hda. Cadena, Quincemil, 1000 m (9 FMNH). **Junin:** Chanchamayo, 1000 m (2 BM, including holotype of *A. glaucus*); Huacapistana (1 FMNH). **Puno:** Río Inambari, 670 m (3 AMNH); Santo Domingo (1 AMNH); Yahuaramayo, 366 m (1 BM, 1 USNM).

***Artibeus gnomus*—**Total 104. **BRAZIL. Mato Grosso:** Serra do Roncador, 264 km N (by road) Xavantina, 533 m (17 USNM). **Pará:** Belém, Sta. A, IPEAN (7 USNM); Belém, Utinga (5 USNM); Belém, Benevides (2 USNM). **ECUADOR. Pastaza:** Canelos, upper Río Bobonaza (1 AMNH). **GUYANA. E. Berbice District:** Wikki River (3 USNM). **Mazaruni-Potaro District:** Issano Road, 12 mi W of Bartica-Potaro Road (1 USNM). **PERU. Loreto:** 59 km SW Pucallpa (1 USNM); Santa Rosa, Alto Ucayali (10°42'S, 73°50'W) (2 AMNH). **VENEZUELA. Bolívar:** El Manaco, 59 km SE El Dorado, 150 m (12 USNM); Km 38, SE El Dorado, 100 m (1 UCV); Los Patos, 28 km SE El Manteco, 150 m (4 USNM); Río Supamo, 50 km SE El Manteco, 150 m (1 USNM); Salto Chalimaha, Río Paramichí, Río Paragua (1 UCV); Salto Ichun, Río Paragua (2 UCV). **T.F. Amazonas:** Belén, Río Cunucunuma, 56 km NNW Esmeralda, 150 m (2 USNM); Boca Mavaca, 84 km SSE Esmeralda, 138 m (1 USNM); Caño León, Cerro Duida, 325 m (1 AMNH); Capibara, Brazo Casiquiare, 106 km SW Esmeralda (1 USNM); Esmeralda, Cerro Duida, 325 m (3 AMNH); 14 to 65 km S, SSE, and SSW Pto. Ayacucho, 119–161 m (16 USNM); Río Mavaca, 108 km SSE Esmeralda, 140 m (7 USNM); San Juan, Río Manapiare, 163 km ESE Pto. Ayacucho, 155 m (6 USNM); Tamatama, Río Orinoco, 135 m (7 USNM).

***Artibeus phaeotis*—**Holotypes of *A. phaeotis* and *A. ravus*, plus hundreds of other specimens from Mexico, Central America, and NW South America.

***Artibeus pumilio*—PERU. Loreto:** Masisea, Tushemo, Río Ucayali, 328 m (1 BM, holotype of *A. pumilio*).

***Artibeus watsoni*—PANAMA. Chiriquí:** Bogava, 250 m (5 BM, including holotype of *A. watsoni*); Progreso (34 USNM); Puerto Armuelles (2 USNM).

REMARKS—In previous publications of SVP, *Artibeus gnomus* has been known as "*Artibeus* sp. A".

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